

## COURTSHIP AND ALTERNATIVE MATING TACTICS IN A SOCIAL SPIDER<sup>1</sup>

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### ABSTRACT

Males of a social theridiid spider, *Achaearanea wau* Levi, have a prolonged and complex courtship in the communal web. They also mate opportunistically, by copulating with females engaged in molting or feeding. Ritualized aggression occurs between males during attempts to mate with molting females and during courtship. I describe the courtship, mating, and agonistic behaviors observed in *A. wau* and the conditions in which the different behaviors occur and discuss ways in which the social organization may have modified mating behavior. This is the first detailed description of the mating system of a highly social species of spider.

### INTRODUCTION

Mating behavior and the mating system are influenced by social organization (Thornhill and Alcock 1983). Sexual selection in social species, as in nonsocial ones, may produce (1) exaggerated traits associated with mating and (2) synchronization of mating effort. Because communication in social groups is complex and there are more opportunities for repeated interactions among individuals, we might expect sociality to favor greater ritualization of both courtship and agonistic behaviors (than in nonsocial species). Therefore, the mating tactics of a social species should be instructive in elucidating the factors that influence the evolution mating systems.

Many species in which complex male courtship displays occur have one or more alternative mating tactics, used either by different kinds of individuals or in different circumstances (Thornhill and Alcock 1983). (I use tactics throughout to mean complex behavior sequences). Often males attempt to obtain matings without engaging in time-consuming (and often risky) courtship displays. This may be done either by sneaking copulations or by mating with females while they are engaged in some other activity or are incapable of preventing the male's advances. Such tactics are often referred to as "opportunistic mating" (Robinson and Robinson 1980; for reviews of alternative mating behaviors, particularly in invertebrates, see Blum and Blum 1979, Thornhill and Alcock 1983). Alternative mating behaviors were described in several species of solitary spiders (Robinson

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1978a, Robinson and Robinson 1980, Christenson 1984), but have not been observed previously in social species.

Only fragmentary accounts are available of mating behavior of social spiders (Robinson 1978b, Jacson and Joseph 1973); therefore, a detailed description of mating in the social theridiid spider, *Achaeearanea wau* Levi is warranted. I describe here the different mating behaviors and the conditions in which they occur, and discuss the possible functions of the different tactics and the evolution of the mating system of *A. wau*. I show that (1) mating behavior in *A. wau* is complex, involving stereotyped courtship and at least two alternative tactics that do not involve courtship, and (2) mating is synchronized and spatially localized in the colony. A quantitative analysis of alternative mating tactics is provided elsewhere (Lubin, ms).

## METHODS

**Natural History.**—*Achaeearanea wau* Levi (Theridiidae) is a social spider found in montane forest and forest edge in Papua New Guinea (Levi et al. 1982). The communal web of a colony consists of a nonsticky, horizontal sheet with a tangled maze of nonsticky threads (the barrier web) above it and one or more curled-leaf retreats suspended in the barrier web by strong threads (Fig. 1). The spiders sit in or below the leaf retreats during the day and are active mainly at night; prey capture and web maintenance activities are cooperative, feeding takes place in leaf retreats and spiders share prey. Females and their offspring overlap in time. Females tend eggsacs and capture prey for the young (of other females as well as their own). Accounts of colony structure and activities of spiders are provided elsewhere (Lubin 1982, Lubin and Crozier 1985).

*Achaeearanea wau* colonies have discrete, overlapping generations. No more than two generations are present in a colony at any time, and adults of consecutive generations do not overlap. Females mature at the seventh instar and most females in a colony mature at the same time. Males are smaller than females (body length: males 2 mm, females 4.5 mm) and mature at the fifth instar, about 3-4 weeks before the females (Table 1). The sex ratio is skewed towards females, with about six females per male. Courtship and mating activities take place in the parent colony over a period of 3-7 weeks, but most of the activity is concentrated during a 2-3 week period (Table 1). Females produce one or two eggsacs each, one to two weeks after mating. Dispersal is by means of mass swarming of adult females and does not occur in every generation (Lubin and Robinson 1983).

**Observations and Analyses.**—Observations of courtship and mating behaviors were of spiders in colonies that were maintained in semi-captivity in the gardens and coffee plantations of the Wau Ecology Institute (Wau, Morobe Province, Papua New Guinea, elevation ca. 1100 m) and in natural populations in the vicinity of Wau.

Colonies were collected from natural populations and released onto open wooden frames (60x60x60 cm) provided with wire-mesh screens across their lower faces (used to collect prey remains and other spider rejects) and perched on legs at about 1.5 m above ground. There was no need to enclose the spiders completely; when the collapsed web with leaf retreats (brought in from the field)



Fig. 1.—Web of *A. wau* showing the sheet (S), barrier web (B), and curled-leaf retreats (L).

was suspended from the frame, the spiders generally rebuilt the communal web during the following two nights, sometimes attaching lines to the surrounding vegetation as well as to the wooden frame. The colonies in semi-captivity were in a habitat similar to the forest edge and treefall clearing habitats that they normally occupy. The colonies were checked at least twice a week (generally daily) to determine the onset of the various developmental stages (Table 1).

Courtship activities were observed in 10 colonies during the period October 1979-January 1981. Observations of males in these colonies were made for periods of 1-20 days per colony, for a total of 60 days. Most observations were of unmarked males: males were too small to mark with dots of acrylic paint. I watched an individual male and recorded its activities for periods of 30 sec to 10 min, until he moved out of sight or became inactive. Timed observations of individual males (a total of 678 min for all colonies combined) were supplemented by routine, nightly censuses of spider activity in all colonies. Observations were made mainly at dusk and at night, when the males were most active. I recorded when and where females molted and if they were approached by males, as well as any other activities in the colony (kleptoparasite activity, feeding, etc.). Details of male behavior, particularly the courtship sequences, were observed with the aid of a pair of 10 x 40 binoculars mounted on a tripod and fitted with a +3 diopter close-up lens on one eyepiece. Super-8 movie films and videorecordings (using a SONY AV-3400 videorecorder) were made at night using artificial lighting.

### COURTSHIP AND MATING BEHAVIORS

Sexual activities in *A. wau* include searching for a mate, pre-copulatory displays, female responses to male advances and finally mating (or mating attempts). I also include male-male interactions and sperm induction, as these behaviors occur only in the context of courtship and mating activities.



Table 1.—Chronology of events related to courtship and mating activities in colonies of *A. wau* maintained in semi captivity. (a) A = Mt. Missim, 1500 m; B = Wau Ecology Institute, 1200 m; C = Mt. Kaindi (Kunai Creek), 1700 m; D = Mt. Kaindi (Namie Creek), 1600 m; E = Mt. Kaindi, elevation unknown. (b) Number of days from the first appearance of mature males and females to first observations of courtship or mating activities. Negative numbers indicate that males began courting before females matured. (c) Colony collected while courtship was already in progress.

Colony No.	Origin (a)	Days to First Courtship		Mating Season	
		Male	Female	Month	No. Days
1	A	4	-15	Feb.	39
2	C (c)	—	—	Mar.	—
3	D	28	0	May	26
4	E	29	3	May	28
5	B	28	0	Jun.	22
6	A	17	-6	Oct.	32
7	B	11	1	Nov.	31
8	B	15	2	Dec.	51
9	C	21	0	Dec.	36
10	B	11	-5	Dec.	29

Mean duration of mating season + S.D. = 32.7 + 8.5 days

Courtship and mating took place in the communal barrier web, primarily in the region of the curled-leaf retreats. A male became active and began to search for a female. If he encountered an adult female (sometimes subadult females were apparently not distinguished from adults), he either attempted directly to mate with her (Fig. 2A), or constructed a mating arena and began courting (Fig. 2B). A nearby female sometimes responded to the courtship display by approaching, touching legs with the male and then hanging from a thread in a receptive posture; the male then attempted to copulate. A searching male that encountered a female in the process of molting attempted to copulate without courting (Fig. 2C). Males sparred over molting females, and in certain other contexts as well. The different behaviors are described in detail below.

## MALE REPRODUCTIVE BEHAVIORS

**Sperm induction.**—Sperm induction began with the male cutting out barrier web threads and putting in his own draglines. The sperm "web" of *A. wau* is not a web at all, but a single thread that is reinforced several times. The male then dabbed sperm onto the thread with his abdomen and a shiny, white spot became visible on the thread. While filling the palps, the male was supported in an inverted position by all 8 legs. The palps were filled one at a time, alternating left and right, and repeating the process several times. When first applied to the droplet of sperm, the palp was vibrated rapidly; this was followed by slow pulsating movements. As each palp was removed from the sperm droplet, it was shaken rapidly a few times. The male then remained sitting and passed each palp through the chelicerae (cleaning?), sometimes pausing to wave the palp up and down gently for 10-30 sec. After sperm induction, the male remained sitting and occasionally cleaning the palps for more than 15 min.

Sperm induction was observed on five occasions: twice in the morning and three times in the afternoon and early evening. one male began construction of the sperm web about 10 minutes after a copulation. Charging of palps after a



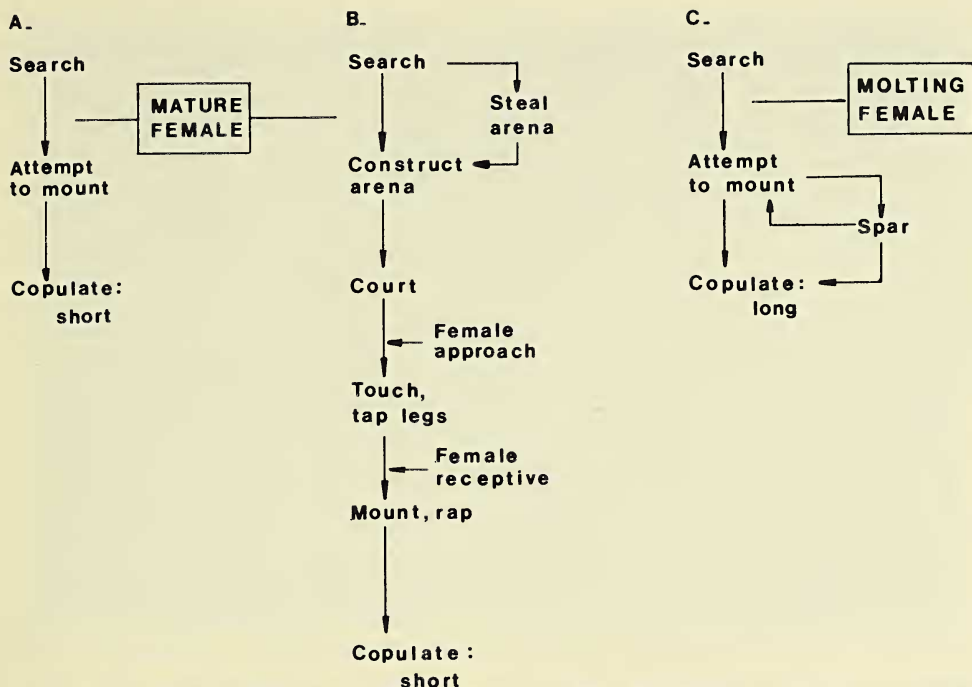


Fig. 2.—Schematic diagram of male mating behaviors, given encounters with mature (non-molting) females (A and B) or with a molting female (C). In courtship sequences with mature females (B), males mount only if females adopt a receptive posture.

copulation has been reported in other spiders (e.g., *Sicarius* sp., Levi 1967). Sperm deposition lasted 15 sec in one instance and about 36 sec in another. Two complete sequences of charging of palps lasted 9 and 17 min, respectively. Each subsequent palp application was of longer duration than the previous one; two such sequences were 23, 27, 40, 62 and 31, 37, 42, 52, sec, alternating palps each time.

**Searching.**—At the beginning of an activity bout, males walked around near and below the leaf nests, and made tapping and rotary movements with legs I, frequently touching females that they encountered. Searching graded into courtship or into attempts to copulate with a female.

Are these male perambulations in the web in fact 'searching' behavior, and are they specifically aimed at finding females? The evidence in support is as follows. First, the tapping and rotary movements of legs I were indistinguishable from exploratory movements used in other contexts (e.g., web-building or approaching foreign objects in the web), which suggests that the spider is receiving tactile and/or chemical cues. Second, the males were active almost exclusively in the immediate vicinity of the leaf nests, where females could be found either feeding or inactive. This is quite unlike the behavior of females, or juveniles or either sex and of males before the onset of sexual behavior: when these spiders became active, they moved away from the leaf nests into the barrier web or onto the sheet where most colony activities (web repair, prey capture) took place. Finally, during "normal" colony activities there was little physical contact between individuals, whereas searching males frequently touched females and indeed, moved from one female to the next.

**Courtship: the display.**—Males courted in small lacunae in the barrier web which they prepared just before courting (Fig. 3). The male cut out a small volume of barrier web threads and laid down one or more dragline threads. These threads might be considered functionally equivalent to the mating thread of araneids (Bristowe 1958). Most display courts were situated near or just below the leaf nests. Courtship was not always preceded by construction of mating threads; apparently males displaced one another from display courts, or simply used courts abandoned by other males. In practice, it was difficult to recognize a display court unless one observed the male building it. Small, thread-free spaces occurred naturally in the barrier web (for example, where an insect had been removed from the barrier web) and the male's mating threads were not distinguishable (to the observer) from other silk lines.

The behavior of cutting out segments of the females' web before or during courtship, thereby reducing the capture area of the web, is sometimes interpreted as a mechanism for minimizing the risk to a male of being attacked by the female and treated as prey (e.g., *Fecenia* sp., Robinson and Lubin 1979), or as a means of cutting off the female's escape route from the male (e.g., in *Latrodectus hesperus* Chamberlin and Ivie, Ross and Smith 1979). Neither of these explanations is applicable here, since the females are neither aggressive nor do they show a tendency to escape from the web. More apposite is Rovner's (1968) suggestion that web removal reduces the possibility of interference from other males and isolates the female from extraneous signals (such as those of insect prey) that might interfere with mating.

Courtship involved two distinct displays, abdomen vibrating and twanging, which were sometimes accompanied by tapping and rotary movements of first legs. Abdomen vibrating (AVing) involved high frequency, low amplitude, vertical oscillations of the abdomen from the pedicel. A single oscillation lasted about 1/9 sec (2 frames of super-8 film at 18 fps) and displaced the mating thread by 2 mm. While AVing, all legs rested on threads and only the abdomen moved (Fig. 3). The vibrations induced were probably transmitted via the legs and dragline to the mating thread and thence to threads in contact with the female.

Similar abdomen movements occur as part of the courtship behaviors of other species, e.g., in the linyphiid, *Frontinella pyramitella* (Walckenaer) (Suter and Renkes 1984) and in the theridiids *Achaearanea tepidariorum* (C. L. Koch) (Bonnet 1935), *Teridion pallens* Blackwell (Locket 1926) and *Latrodectus hesperus* (Ross and Smith 1979). In the theridiids *Steatoda* (= *Teutana*) *grossa* (C. L. Koch) and *S. bipunctata* (Linnaeus), stridulatory organs on the abdomen are coupled with abdomen vibrating movements to produce vibrations or clicks (sometimes audible) that may be transmitted through the web (Gwinner-Hanke 1970). A stridulatory organ was not found in *A. wau* males examined under scanning electron microscopy (H. W. Levi, pers. comm.).

Twanging is described by Robinson and Robinson (1980, p. 13) as "a movement on mating threads in which the thread is rapidly tensioned and then the tension suddenly released." Twanging or plucking of threads occurs as a component of courtship in many web spiders (e.g., *A. tepidariorum*, Bonnet 1935; *Teridion pallens*, Locket 1926). In *A. wau*, the male pulled the mating thread by flexing legs I and II and released it suddenly with legs I (and perhaps II), causing a violent backwards jerk of the whole body. Both the spider and the mating



Fig. 3.—Male courting in the barrier web. Note that all legs hold threads.

thread were displaced during a twang which may produce large amplitude oscillations of the mating thread (Fig. 4).

Tapping and rotary movements of first legs occurred during AVing and between twangs. One leg I lightly touched the mating thread or nearby threads in a slow, gentle motion that did not visibly deflect the thread. Sometimes the tapping leg I did not strike a thread and continued to wave about in the air in a circular movement, similar to leg I movements made when walking in the barrier web and searching for females.

Courtship displays followed a stereotyped sequence, always starting with a bout of AVing and followed by alternating bouts of twanging and AVing of variable duration. A few patterns emerge from analyses of Super-8 films of courtship sequences: (1) Twangs were often given in short bursts of 2-4 at a time. Intervals between twangs within a burst were distributed bimodally, with peaks at  $2/9$  to  $1/6$  sec (4-6 frames of super-8 movie film, at 18 fps) and at  $13/18$  to  $5/6$  sec (13-15 frames; Fig. 5A). (2) Bouts of AVing were most frequently  $2/9$ - $2/3$  sec (4-12 frames) in duration, with a mean of 0.77 sec ( $SD = 0.75$ , range 0.06-4.28,  $N = 102$ ; Fig. 5B). No regular pattern could be detected in either the frequency or duration of alternating bouts of AVing and twanging within a display sequence. However, individual variation was not studied.

AVing occurred off the mating thread in two contexts besides during courtship: males AVed while following or attempting to mount females and during male-male sparring bouts (described below). In neither of these contexts was AVing accompanied by twanging.

**Courtship: interactions.**—Are male displays directed at particular females or are they addressed to any female within 'hearing' distance? Searching behavior, placement of the display thread and the display itself all seemed to be directed at one or a group of females. The male investigated several females from close range while searching; the display thread was attached at its proximal end to



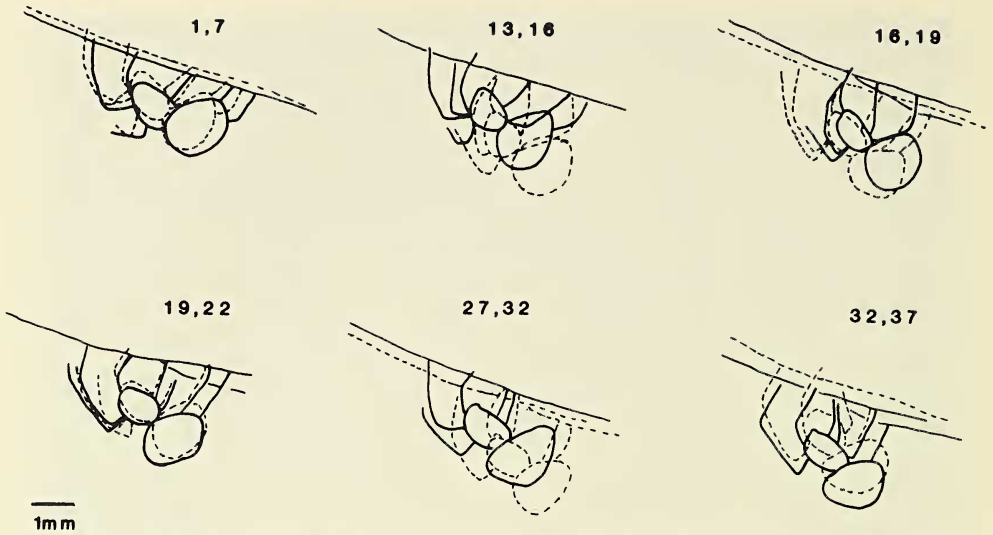


Fig. 4.—Twanging. Drawings based on a sequence of frames from Super-8 movie film. Two frames are superimposed in each drawing, the first in solid lines and the second in dotted lines; frame numbers are shown above each drawing. Note that in some frames not all legs were visible. The backward jerking portion of the twang was seen as a blur on a single frame (15). Two twangs are shown (frames 13-16 and 27-32). A small, forward movement precedes the twang (1-7, 7-13). The vertical displacement of the thread was about 4 mm.

threads on which one or more females rested and while building the display thread, the male frequently approached and touched these females; and finally, the male displayed facing one or more females at a distance of 1-5 cm. Apparently, however, the displays were not perfectly directional; females sometimes approached displaying males from behind or from the side. Courting males responded to frontal approaches by attempting to copulate in 89% of 89 observations, and in only 20% of 56 observations of approaches from other directions ( $\chi^2 = 66.85$ ,  $p < 0.001$ ,  $df = 2$ ).

The behavior of a displaying male on the approach of a female depends on the response of the female (see Female Behaviors). Usually, there was mutual touching and tapping of legs, after which the female adopted an acceptance posture and the male mounted. Sometimes, however, the female approached the male to within 1 cm or less and sat. The male either went up to the female, touched her and resumed displaying, attempted to climb directly onto her ventral side and copulate, or left to search for a new display site. The cues that trigger the different male responses are not known.

Interference from other males during the display resulted in the termination of courtship in nearly 10% of 197 courtship bouts in one colony. After such interruptions, the 'resident' male either resumed displaying or searched for a new site. Likewise, when a courting male failed to attract a female or when a female approached and then rejected the male, he often moved away from the display court and resumed searching.

#### COPULATION AND COPULATION ATTEMPTS

If a female adopted a receptive posture (see below) following the male's display, the male moved to the female's ventral side and drummed on her epigynum with

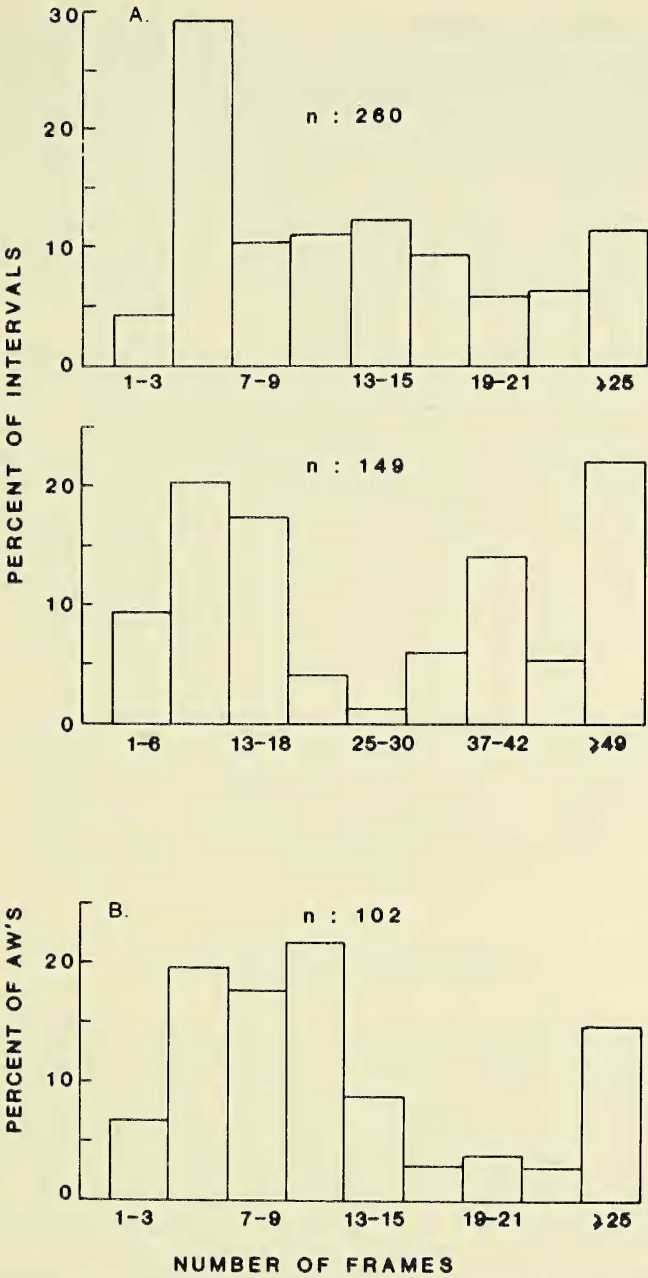


Fig. 5.—Frequency distributions of components of courtship. (a) Intervals between successive twangs, based on Super-8 movie films at 18 fps (upper) and on videorecordings at approximately 30 fps (lower). (b) Durations of abdomen vibrating (AVing), in frames of Super-8 movie film at 18 fps.

the palps, alternating them rapidly. Males also drummed on the epigyna of females that were busy feeding, in attempts to copulate. Montgomery (1903) commented that male *Achaearanea tepidariorum* appeared to have difficulty inserting the palp once the female adopted a receptive posture. This appeared to be the case in *A. wau*. Palpal drumming may be a way of stimulating the female to allow copulation and, as such, is an important part of courtship. Palpal drumming may have a function similar to that of the pre-mating insertions in

*Frontinella pyramitella* (Helsdingen 1965) or the post-mount courtship display of *Phiddipus johnsonii* (Peckham and Peckham) (Jackson 1982).

If successful in stimulating the female, the male inserted one palp and pumping movements of the abdomen could be seen. A male copulated only once, with one palp, and then was usually chased away by the female. Copulations with mature (non-molting) females were of short durations: all but one of nine timed copulations lasted less than one minute, and all were terminated by the female. There was no evidence of a copulatory plug, nor did males break off one of their emboli, although both of these phenomena are known to occur in other theridiids (e.g., Braun 1956).

If a female was not receptive there often ensued a frantic scramble on and around her abdomen, as the males(s) tapped and drummed on her abdomen with his palps and legs and attempted to gain access to her ventral side. This behavior was observed in *A. wau* in three contexts. First, males pursued and attempted to mount females that were attracted initially to the male courtship display, but then rejected the male and moved away. I never observed a copulation following such a pursuit. Second, when copulation attempts were interrupted by another male, both males scrambled around the female as she moved away. Third, *A. wau* males scrambled and sparred with one another on molting females, and even on exuvia of newly molted females and on females that had died during molting (see below).

During copulation with mature as well as with molting females, the male's long axis was parallel to that of the female and the two spiders faced in the same direction. Sometimes, however, the movements of a recently molted female attempting to dislodge a copulating male, caused the male to turn around so that his body was at a right angle to that of the female, or even facing in the opposite direction.

### MALE-MALE INTERACTIONS

There were four possible outcomes to an encounter between two (or more) males: (1) the males ignored one another, (2) they touched one another and one or both moved away, (3) one male chased another away, and (4) they sparred and one eventually fled, often chased by the other. Sparring males tapped, pushed and grappled with one another, using the legs and palps. I never saw injury of any sort to a male as a result of sparring, nor did I see males with missing appendages. Sparring appears to be a form of ritualized fighting and occurred only in the context of male sexual activities. No other form of fighting was observed. Although males matured before females and were thus present as adults in the colony for several weeks before courtship began, neither male-male aggression nor male-male interactions of any other sort, were observed before the onset of the mating season.

Sparring bouts and chases occurred most frequently when one male interfered with courtship activities of another either during a display or while attempting to mate with a female. They also occurred when males encountered one another during searching and when building a mating thread. A searching male was more likely than a displaying male to 'give up' and move away after an encounter (Table 2).



Table 2.—Outcomes of male-male encounters during courtship and attempted copulations (C/AC) and during searching (S), based on observations of males in 10 colonies. Group sparring events are excluded. Male #1 is the instigator of the encounter (in searching males) or the resident in encounters during C/AC. Possible outcomes were: either male #1 or male #2 left first, or there was no clear winner (both males left or both remained inactive). Expected values are in parentheses. The null hypothesis that there is no difference in the outcomes of encounters of C/AC and S males is tested (G test, df=2). [ $G = 15.713$ ,  $p < 0.005$  (two-tailed)].

Male #1	First male to leave			Totals
	Male #1	Male #2	Both/Neither	
C/AC	22 (23.2)	45 (34.0)	15 (24.8)	82
S	21 (19.8)	18 (29.0)	31 (21.2)	70
Totals	43	63	46	152

As a mating tactic, male interference and attempts to displace courting males appear to be unsuccessful. In no instance did I observe an interfering male gain access to a female ( $N = 152$  attempts) and these contests generally ended with one or both males moving away. Nonetheless, there may be other advantages: an interfering male may disrupt the courtship display of another male sufficiently to cause him to move away, whereupon the invading male can usurp the display site. Displacements of this sort occurred, although more frequently the displaying male chased the intruder away (Table 2). The possibility of size advantage in these contests (Rovner 1968, Suter and Keiley 1984) was not examined.

Intense sparring bouts occurred over molting females and sometimes clusters of males could be seen sparring over a molting female (Fig. 6) or over a recent exuvium. The latter behavior suggests that chemical cues present in the molt trigger male copulation attempts. A phenomenon that remains largely unexplained is that of ‘spontaneous’ clustering of sparring males, with no female to be seen nearby, nor even an exuvium to indicate that a molting female had been there. Males entered a cluster, engaged in pushing and shoving matches, left to sit in nearby threads or walked about tapping nearby females, and then returned to the cluster to resume sparring. Such clusters persisted, with changes in the number and identities of the contestants, for up to an hour,

How do such sparring contests start and what attracts males to them? Many sparring contests (55% of 29 contests observed in one colony) began in the presence of a molting or recently molted female or her exuvium, but continued long after the females had moved away. Clusters of sparring males also shifted location in the web as males left and entered them. Perhaps males are attracted to such clusters initially by chemicals produced by molting females and, later, by cues (chemical or vibrational) from the sparring males themselves.

Two explanations for the occurrence of these group sparring bouts are suggested: (1) that they are a product of a state of high sexual “excitement” on the part of the males and the likelihood of finding a molting female in the center of such a cluster, and (2) that they involve the establishment of a dominance hierarchy among males that, in the long run, determines access to females.

The occurrence of clusters of sparring males mainly early in the mating season when molting females are present in colonies supports both explanations. During this period males may be highly motivated to search for and attempt to mate with molting females (see following sections for the reasons why this might be the case). Likewise, a dominance hierarchy would be established early in the period of sexual activity, as females are maturing and molting to adults. The presence

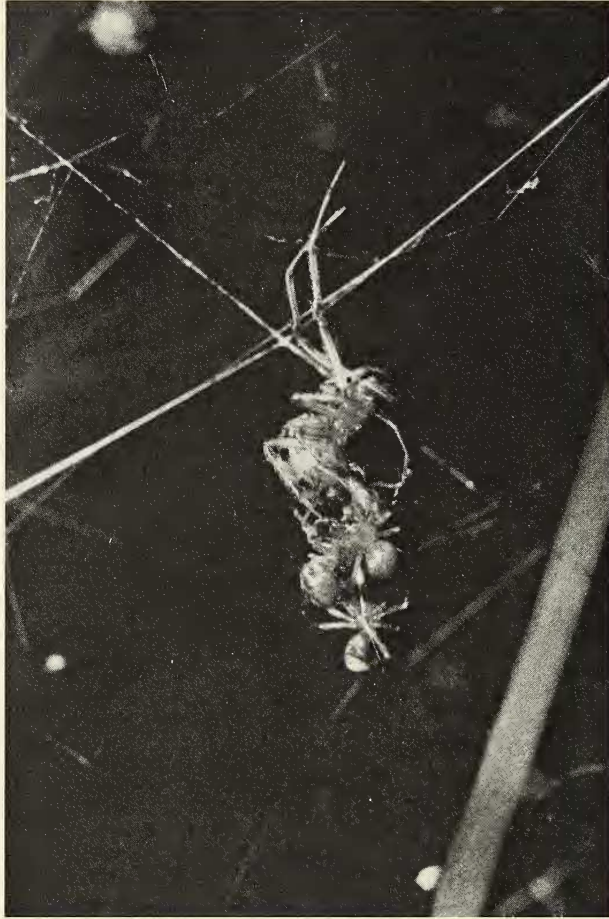


Fig. 6.—A group of males of *A. wau* sparring over a recently molting female. The female is able to move her legs and is pushing the males away.

of a dominance hierarchy implies individual recognition, a possibility which was not examined. Further observations, particularly of marked males, are clearly necessary.

AVing occurred in the context of male aggression (1) when several males attempted to mate with a molting female, (2) during sparring bouts and (3) during interference with a male that was courting or attempting to copulate. AVing during male-male interactions appeared to be of lower frequency and higher amplitude (slower and more pronounced oscillations of the abdomen) than while courting a female. Possibly different messages are conveyed by differences in the frequency and amplitude of the vibrations produced in AVing. Abdomen twitching was observed in both courtship and male aggression in a salticid spider (Jackson 1978a) and, indeed, the use of similar signals of different intensities in both courtship and male-male aggression is common in many animals (c.f., Cade 1979).

## FEMALE BEHAVIORS

Mature, non-molting females responded to male courtship by tapping him with legs I and II. If the female was receptive, she adopted an acceptance posture, in which she hung from the threads (the male's mating threads?) by legs IV, while legs I and II were held together either flexed over the cephalothorax or downward and away from the body. As the male attempted to mate, the female often held him with one or both legs III.

If a male persisted in drumming on the female's ventral side without succeeding in inserting the palp, the female then began to push him away with the legs, at first gently, then more sharply and sometimes ending in a lunge at the male and an apparent attempt to seize and bite him. The male reacted to the pushing by either attempting to follow the female and scramble back onto her or moving away, and to the lunge, by dropping several centimeters into the lower barrier web. I never saw a female actually seize a male.

Much of the time, nearby females showed no response to courting males. When a searching male approached and touched a female, she either remained motionless or moved away. If the male persisted in following, she moved into the lower barrier threads, or even under the sheet, pushing the male away with her hind legs. Later in the reproductive season, females aggressively lunged at courting or pursuing males and chased them into the lower barrier web. As in the case of male-male sparring, I never saw any damage to a male thus 'attacked' by a female. Bonnet (1935) described similar behavior in *Achaearanea tepidariorum* where older, mated females chased courting males aggressively, but never harmed them.

## COPULATIONS WITH MOLTING FEMALES

Molting females hung by legs I-III, while their flexed legs IV held onto the web near the cephalothorax. After molting, the spider remained hanging by a thread from the exuvium in an inverted posture, such that all legs hung down and were slightly flexed. One molt from last instar to adult female lasted 23 min from the start of pumping movements to the first coordinated leg movements of the adult female. During this period the female was defenseless. Another 22 min elapsed before the female broke the attachment to the exuvium and moved away.

During the molt from penultimate instar to adult, females were sometimes mated by one or more males. As many as 15 males were observed clustered around a single molting female. I saw four instances of multiple copulations, one of which involved four males in succession. Sometimes one male succeeded in mating 2-3 times with the same molting female. This suggests that the male did not transfer all of the sperm in one palp in the first insertion. Copulations with molting females were terminated by the male, or as a result of interference from other males, and were of longer duration than copulations with mature females following courtship (molting females:  $n = 19$ , median = 60 sec, range 15-540 sec; mature females:  $n = 9$ , median = 18 sec, range 6-129 sec;  $0.01 < p < 0.025$ , Wilcoxon two-sample test).

Of 140 females observed molting in 8 different colonies, 40.7% were discovered by males, and of these 59.6% were mated during molting, corresponding to 24.3%



of all molting females. Females that molted at night in the vicinity of the leaf retreats were more likely to be discovered and mated than were individuals that molted during the day and away from the retreats. In one colony in which molting females were observed throughout the mating season, 4 of 6 females that molted at night were discovered by males who attempted to copulate with them, whereas only 14.8% of 81 females that molted during the day were discovered by males. Furthermore, about 2/3 of the molting females (109 of 152) were observed during the day (0600-1600), a distribution that reflects a real preference for molting during the day. Of 64 females that molted near leaf retreats, 52% were discovered by males who then attempted to copulate with them, whereas only 1 (2%) of 45 females that molted in the upper barrier web was discovered ( $\chi^2 = 29.81$ ;  $p < 0.001$ ,  $df = 1$ ).

There is an immediate risk to a female to being discovered and copulated with during molting, aside from possible long-term disadvantages involving loss of reproductive fitness. As the female's exoskeleton begins to harden, it becomes difficult for a copulating male to withdraw the embolus and he may become 'stuck.' Upon separating one such pair, I noticed a sticky secretion of unknown origin covering the embolus and epigynum. As soon as the female was capable of moving, she attempted to free herself from the copulating male by pushing him with her legs III and IV. The male at first remained passive, then attempted to withdraw the palp. Pairs often remained stuck for more than 12 hours. Males became stuck in 40% of 40 observed copulations with molting females and on at least four occasions (10% of all matings with molting females), both members of the pair died while still *in copula*.

The risk of discovery by males during molting may be a strong selective pressure for molting in locations and at times when males are least likely to be active. Females molting during the day in the upper barrier web may be exposed to risks of predation (by kleptoparasitic spiders of the genus *Argyrodus* (Theridiidae), mimetids and salticids as well as by wasps and birds.) Although I did not observe predation directly, I did find *Argyrodus* feeding on dead *A. wau* individuals in the barrier web. Furthermore, females were found in the upper barrier threads during the day only in two circumstances: during rare excursions to capture prey or during the last molt. All other (pre-adult) molts occurred in the vicinity of the leaf nests, and predominantly at night.

Matings with molting females give the appearance of forced copulations (a term less emotionally charged than 'rape;' Thornhill and Alcock 1983). First, molting females have no control over the mating; second, as soon as females can move, they attempt to free themselves of the male; and third, females molt in circumstances that minimize the chance of being found by males. Forced copulations may be undesirable for females because (1) they allow no choice of mate and (2) they carry a high risk (higher for the females, who loses all, than for the male, who may have already mated with other females).

## DISCUSSION

**Variable Mating Tactics.**—Intraspecific variation in male mating tactics is to be expected when the 'interests' of males and females do not coincide exactly, as is the case when females are choosier than males in accepting mates (Maynard

Smith 1982). The most thoroughly studied example of variable male mating tactics in nonsocial spiders is that of a salticid, *Phiddipus johnsonii* (Jackson 1977, 1978a). Males of this species have three distinct tactics: they may court females outside their nests with a species-typical, visual display; search for and mate with females in nests, using vibratory courtship only; or cohabit in nests of subadult females and copulate with a minimum of ceremony when females molt to maturity. Unlike *A. wau*, females of *P. johnsonii* can terminate copulations both in the nest and outside it. Thus, although males have alternative mating tactics which differ in their probabilities of success and in the durations of the resulting copulations, there is apparently no tactic by which males circumvent female control of mating.

In many araneids that have large sexual size dimorphism (e.g. the Nephilinae and some species of *Argiope*), the small males either court the female from a distance on her own web, wait to copulate when the female is busy with prey, or cohabit in webs of subadult females and copulate as soon as the female molts to adulthood (Farr 1977, Robinson and Robinson 1980, Alcock 1984b). The tactic of waiting until the female is feeding before approaching occurs in many species, e.g. *Meta segmentata* (Clerck) (Araneidae), *Zosis geniculatus* (Oliver) (Uloboridae), and *Pisaura mirabilis* (Clerck) (Pisauridae), where the male provides a 'gift' of food before copulating (Gerhardt 1927, Bristowe 1958, Blanke 1974). Although females control mating in these cases, the likelihood of the male being rejected may be reduced. Matings with recently molted females have been reported sporadically in the literature, e.g. in a gnaphosid, *Drassodes lapidosus* (Walckenaer) (Bristowe 1958, p. 119) and a clubionid, *Clubiona robusta* L. Koch (Austin 1984). It is not clear from these reports if females are indeed capable of rejecting males under these circumstances.

In these examples and in *A. wau*, a species-typical male courtship tactic is replaced by a more direct tactic under specific conditions, namely, when the likelihood of being rejected by the female is reduced because she is either occupied or incapable of doing so. In contrast to the examples cited above, opportunistic mating in *A. wau* takes an extreme form of forced copulation of females that are in the process of molting (and are completely defenseless), and often by several males in succession. The frequent occurrence of these behaviors in *A. wau* (Lubin, ms.) suggests that female choice acts to increase the variation in male mating success and that this provides strong selection on males to adopt alternatives to courtship.

**Male Fighting.**—Male-male fighting occurs as well in other web-building species, particularly in those in which males cohabit in females' webs before or after copulation (or both). Males of *Nephila clavipes* (Linnaeus) for example, fight for a position at the hub of the female's web (where access to the female is easiest) and interfere with one another during mating attempts (Farr 1977, Christenson and Goist 1979, Vollrath 1980). In the linyphiid, *Frontinella pyramitella*, a male on a female's web defends it against intruding males before and after he copulates (Austad 1982, Suter and Keiley 1984) as may be the case in some pholcids (Eberhard and Briceno 1983). Ritualized aggression occurs in all of these species. Often contests are settled before any direct contact is made and, if fighting breaks out, damages to the contestants occur infrequently. Austad (1982) and Suter and Keiley (1984) suggested that intruding males of *F. pyramitella* are often unable to assess accurately the ability of the resident male

to defend the web and may do so only by increasing the intensity of the aggressive interaction up to the point of a physical contest.

Male-male interactions in *A. wau* differ from those described above: of the three types of interactions seen in *A. wau*—interference and displacement during courtship and mating attempts, fights over access to molting females and group sparring contests—only the first is similar to behaviors seen in non-social species. Nonetheless, sparring over molting females and group fights may also be derived from male-male interactions typical of non-social species. The highest intensity interaction seen between males of *A. wau* was sparring, a ritualized fighting that apparently never caused damage to the participants and at most resulted in one male chasing another away. Sparring bouts were often preceded by, and interspersed with, AVing, which in this context appears to be an aggressive signal of lower intensity. Escalation of aggression from AVing to sparring carried virtually no immediate risk of damage to the contestants in this social species; there already exist strong inhibitions to damaging one another. The outcome of a contest may depend on the stamina or persistence of the contestants rather than on their ability to do damage. The reward may be immediate access to a molting female, or as suggested earlier (and if individual recognition occurs), a higher rank in a male dominance hierarchy which could determine access to females later in the season.

**Evolution of the Mating System of *Achaearanea wau*.**—Comparable studies of mating behaviors of other social spiders are lacking. Krafft (1969) observed a male *Agelena consociata* Denis (Agelenidae) drumming his palps (on the web?) as he approached a female, but the female moved away; *Mallos gregalis* (Simon) (Dytinidae) males courted by plucking the web and twitching their abdomens, but the mating system was not described (Jackson 1978b); there are no published observations of courtship or mating behavior in another social theridiid, *Anelosimus eximius* Simon, although this is perhaps the best studied of all the social spiders (Brach 1975, Vollrath 1982, Vollrath and Rohde-Arndt 1983, Tapia and de Vries 1980, Christenson 1984). However, Vollrath (pers. comm.) observed a male *A. eximius* fight with another male that was attempting to mount a female. Clearly, none of these social species exhibits the frenetic, synchronized mating season seen in *A. wau*. *Achaearanea wau* is apparently unique among the social species studied until now in that (1) it has a communal mating season (2) males have prolonged and complex courtship, (3) forced copulations are common, and (4) males engage in ritualized sparring contests. Can these behaviors be explained in the context of the social biology of *A. wau*?

The synchronous, communal mating season in *A. wau* is a consequence of colony dynamics and life history. New colonies are established by means of synchronous swarming of mated females (Lubin and Robinson 1982). The stage of a colony in its life cycle, rather than seasonal events, determines the timing of swarming. Communal brood defense also imposes a degree of synchrony: several days before females are ready to lay eggs, they remove the capture web, leaving only the leaf nests supported by strong guy threads. The females hang their eggsacs inside the leaf nests, seal the openings and brood the eggsacs for 1-2 weeks. Those females that cannot produce eggsacs during this period (due perhaps to lack of resources) are unlikely to reproduce successfully later (unpublished data).



The courtship of *A. wau* males remind one of the displays of males in leks, and indeed, shares some of the characteristics of lekking behaviors. Males defend small arenas that are used exclusively for courting females and copulating with them; these arenas are concentrated in a relatively small area of the spider's home range (i.e., the colony); and, a female may visit (and perhaps compare) many displaying males during a short period. Most lekking vertebrate (c.f. Bradbury 1981) and some lekking social insects (e.g., harvester ants; Holldobler 1976), use traditional lekking sites. *Achaearanea wau* males, however, change courtship arenas frequently and, indeed, the display site itself may be of little importance except in relation to the position of females in the web.

'Lekking' in *A. wau* males can be understood in the contexts of male mating strategy and the same colony life history characters discussed above. Given that a male's sole investment in his offspring is sperm, his best strategy is to put all his efforts into finding mates and copulating with them. Finding females in the colony presents little difficulty, particularly when females within a colony mature simultaneously. Consequently, during a relatively short mating season, males display vigorously and almost incessantly in sectors of the colony in which receptive females are most likely to be found.

Both female choosiness and male eagerness might select (by means of sexual selection) for elaborate and persistent male displays. Furthermore, given the female's apparent reluctance to accept mates, males should adopt opportunistic mating tactics whenever possible as a means of circumventing female choosiness (see above). In this respect, copulations with molting females may be particularly advantageous (in spite of the risks), since a male may be able to completely fill a female's spermathecae and ensure that all of her offspring will be his own. As molting females are a scarce resource, males are expected to compete for them and fight over them.

The evolution of this mating system from one of a less social or solitary theridiid must remain speculative, given the paucity of comparable observations of other species. *Achaearanea wau* shares certain mating behaviors with other theridiids (*Achaearanea tepidariorum* is the best known example), including elements of the courtship displays (AVing, twanging and post-mount rapping); the occurrence of numerous, short copulations that are generally terminated by the female; and a relative lack of aggression between females and cohabiting males (Bonnet 1935; Montgomery 1903). In addition, males of both *A. tepidariorum* and of a subsocial species, *A. mundula* (L. Koch), congregate on webs of receptive adult females and often cohabit their webs for several days. I predict that male-male interactions and competitive male displays occur in these species, although perhaps less ritualized and less frequent than in *A. wau*.

The differences between *A. wau* and these solitary or subsocial species are related specifically to the social adaptations discussed earlier, low fecundity, skewed sex ratios and dispersal by swarming of adult females resulting in developmental synchrony within colonies. I propose that the unique mating system of *A. wau* is the result of the modification of a 'traditional' theridiid mating system to accommodate these social adaptations.

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